FACTORS AFFECTING THE DISTRIBUTION OF FRESHWATER FISHES ESPECIALLY IN ITALY

by

Pier Giorgio BIANCO (1)

ABSTRACT. - Factors and events affecting the dispersion of native freshwater fishes in Italy and other peri-Mediterranean countries are investigated by analyzing their original distributions. Present day ranges are the result of several factors including the ecology of the species and the palaeoecology and palaeogeography of the area. Main routes of dispersion for primary (*sensu* Myers, 1938), cold-adapted riverine fishes were probably by river captures, while warm-water riverine and lacustrine species spread as a result of confluences in lowlands. In Italy, several cold-adapted riverine species are shared with the Danubian district and are assumed to be of Pleistocene origin. Most endemics, with small ranges and sometimes shared with the western-Balkans, belong to the category of warm-water riverine or lacustrine species. Some of those have probably been isolated since the Middle Miocene (10-15 Ma), others penetrated Italy during the Messinian "Lago Mare" phase of the Mediterranean (5 Ma). Present distribution patterns seem the result of glacial-time events. The last glacial, Würmian, Po extended phase (15-18,000 YBP), played a major role in dispersion into Italy and exchanges with the western-Balkanic district. However, human interference with fishes, especially during the last 60-80 years, has obscured the original ranges and the faunal compositions of every river basin.

RÉSUMÉ. - Les facteurs et les événements qui ont déterminé la dispersion des poissons d'eau douce d'Italie et des autres pays péri-méditerranéens sont recherchés en étudiant des modèles de distributions originales. La distribution actuelle est le résultat de nombreux facteurs comme l'écologie des espèces, la paléoécologie et la paléogéographie de l'aire. Les routes principales de dispersion des poissons réophiles primaires d'eau froide (au sens de Myers, 1938) résultent probablement de la capture de rivières alpines, tandis que les poissons d'eau tempérée ont utilisé les confluences dans les régions collinaires ou en plaine. En Italie, de nombreuses espèces d'eau froide sont communes avec le district danubien et sont considérées comme des dérivés pleistocéniques. La plus grande partie des poissons endémiques, ayant des aires de répartition réduites et quelquefois communes avec la région balkanique, sont des formes d'eau tempérée. Quelques-unes ont été isolées probablement au Miocène moyen (10-15 MA), d'autres ont pénétré en Italie pendant la phase messinienne "Lac Mer" de la Méditerranée (il y a environ 5 MA). Les distributions actuelles semblent être le résultat des événements glaciaires. La phase extensive du Pô, pendant la dernière glaciation du Würm (il y a 15 à 18000 ans), a joué un rôle très important dans la dispersion en Italie et les échanges avec la péninsule balkanique occidentale. Cependant l'interférence humaine sur les poissons d'eau douce, surtout avec les introductions pendant les 60-80 dernières années, a obscursi la distribution originelle des espèces et la composition faunistique dans presque toutes les rivières.

Key-words. - Freshwater fish, Italy, Zoogeography, Palaeomediterranean events, Native ranges, Human influences.

According to salinity tolerance, four divisions of freshwater fishes may be currently recognized in the Italian fauna: 1) Primary: taxa which originated and spread in freshwaters (mostly the Ostariophysi); 2) Primary-like: strictly freshwater species of marine origins

(1) Dipartimento di Zoologia, via Mezzocannone, 8, Università, 80134 Napoli, ITALY.

which show (or share) a distribution similar (or in common) with one or more species of the primary division (for istance several freshwater Gobiidae from eastern Mediterranean drainages; 3) Secondary (mostly the Cyprinodontidae); and 4) Peripheral (recent marine derivates and diadromous taxa) (Myers, 1938; Banarescu, 1990; Bianco and Miller, 1990). Each group follows a distinct mode of dispersal, but species belonging to the first two divisions mostly spread according to historical events in the hydrographic network. Further, in relation to temperature tolerance, three ecological categories of freshwater fishes may be distinguished: a) Cold-adapted species such as trout (*Salmo sp.*), charr (*Salvelinus sp.*), bullheads (*Cottus sp.*), and the minnow *Phoxinus phoxinus*, occupying the mountain region of a river and where the maximum summer temperature is about 12-14°C. b) Moderately cold-adapted species including the grayling *Thymallus thymallus*, lampreys, barbel (*Barbus sp.*), chub (*Leuciscus cephalus*), and the minnow-like *Leuciscus souffia muticellus*, in foothill reaches where summer temperature is about 16-18°C. c) Warm-adapted species such as rudd (*Scardinius sp.*), roach *Rutilus pigus, R. aula* and *R. rubilio, Chondrostoma soetta* and *C. genei*, and *Perca fluviatilis*, which live mostly in the lowland reaches, in lakes, rivers and streams where summer temperature may reach 25°C or more.

Freshwater fish in italy

A number of hypothesis may be advanced to explain the origin and dispersion of freshwater fishes in Italy and other European areas of the Mediterranean. In Italy, the native fishfauna is composed of elements possibly derived by several palaeogeographic and palaeoecological processes which have taken place from the Middle Miocene (Pannonian) to last Würmian glaciation and into historic times. I considered as "ancient" any Miocene or pre-Miocene event, and as "recent" the events happened during the Pleistocene period. In addition, mankind, since the Roman period (or before), has altered the natural distribution of several species. Recently, as a result of more than thirty years of transplantation, the original distribution of native species has become even more obscured (Bianco, 1995). Nevertheless, Bianco (1987, 1990) recognized two chief natural ichthyogeographic districts: the Padano-Venetian district (basins of middle and upper Adriatic sea to the north of the rivers Vomano (Italy) and Krka (Dalmatia), and the Tuscano-Latium district which includes the Serchio, Arno, Ombrone and Tiber basins on the Tyrrhenian slope of Italy (Fig. 1: 7, 8).

FACTORS AFFECTING THE NATURAL DISTRIBUTION OF PRIMARY AND PRIMARY-LIKE FRESHWATER FISHES

EUROPEAN-MEDITERRANEAN

Ancient

The pre-Miocene and Upper Miocene (till to 35-40 Ma) freshwater fish-fauna of Europe was dominated by primitive components. Families including the Lepisosteidae, Amiidae, Notopteridae and Umbridae from the German Eocene (Gaudant, 1988, 1993), bear witness to an ancient connection between Europe and North America, while several percoids seem to be principally related to fish at present living in the Australian Region. In the Upper Miocene, the dominant freshwater fishes (genera *Palaeolebias* and *Mikroumbra*) (Reichenbacher and Weidmann, 1992) are unrelated to the modern European fish-fauna. The fossils related to the Recent Danubian forms are apparently younger. The

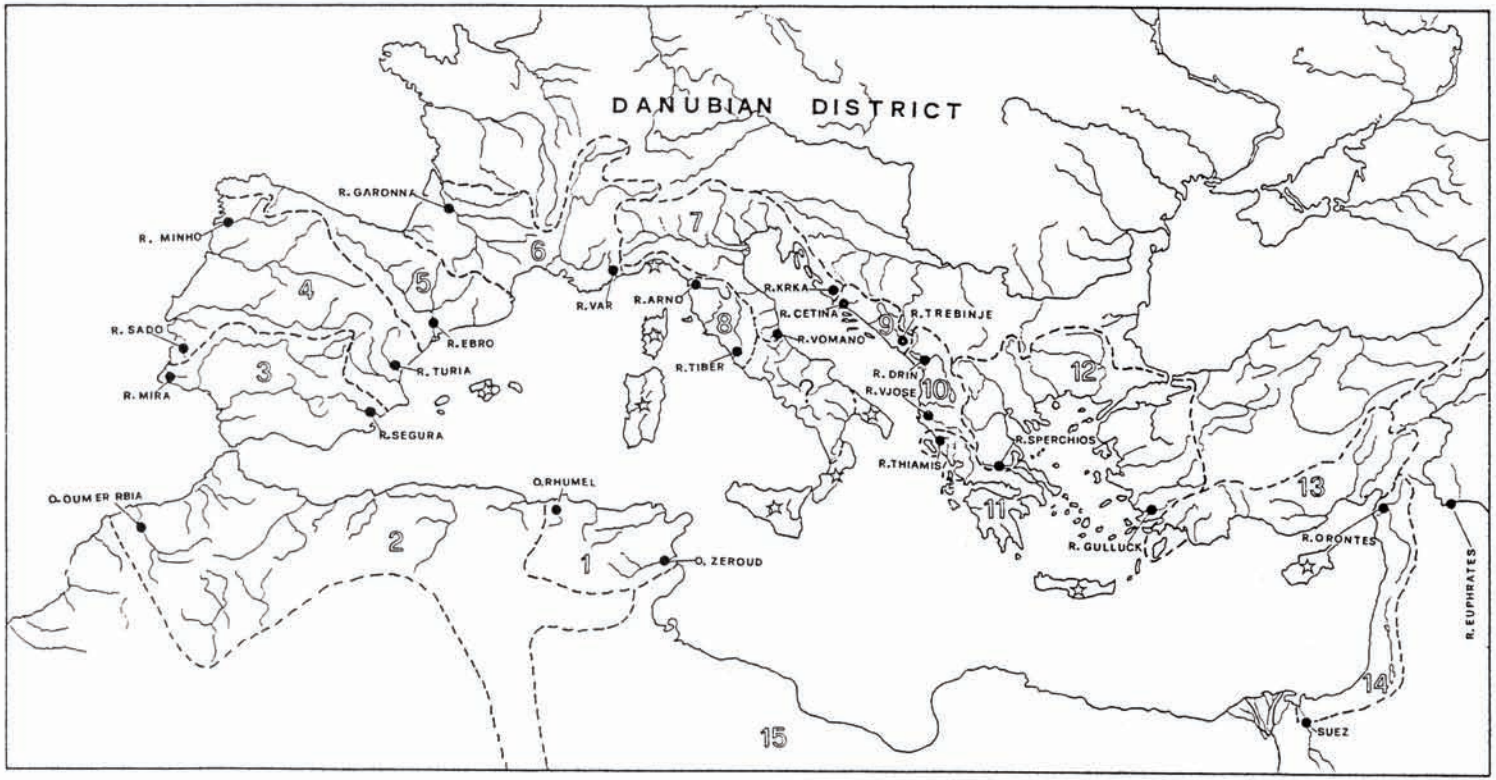

Fig. 1. - The 15 perimediterranean districts based on distribution of endemic freshwater fishes. The rivers (R) and the Wadi (O) reported are those involved in district delimitation. 1) Tunisian; 2) Maghrebo-Algerian; 3) Southern Iberian; 4) Central Iberian; 5) Ebro-Cantabric; 6) Southern France; 7) Padano-Venetian; 8) Tuscano Latium; 9) Dalmatian; 10) Albanian; 11) Western Greece; 12) Aegeo-Macedo-Anatolian; 13) Anatolio-Mediterranean; 14) Levantine; 15) Saharo Mediterranean. Continental lands and islands marked by stars are without native primary freshwater fishes. In southern Italy (?) human interference has obscured the local composition of the fish fauna (from Bianco, 1990).

modern European fish-fauna is mostly of Eastern Asiatic origin (Banarescu, 1973; Almaça, 1978; Bianco, 1990) and has dominated Central Europe and some northern regions of southern peninsular Europe since the Middle Miocene (Doadrio, 1981; Martini, 1983; Gaudant, 1989).

In southern peninsular Europe and north-west Africa, fossil remains related to European fishes are absent, or no older than Messinian (about 5 Ma) (Greenwood, 1974; Azzaroli and Lazzeri, 1977; Sorbini and Tirapelle Rancan, 1979; Doadrio and Casado, 1989; Gaudant, 1992). In the peri-Mediterranean areas, the absence of pre-Messinian fossil European-like primary-fishes, and the present high level of endemic forms confined to restricted ichthyogeographic districts (Fig. 1), has been attributed to a process of dispersion during the "Lago Mare" phase of the Mediterranean (Hsü, 1978; Bianco, 1990). During the Messinian salinity crisis, the desiccated Mediterranean basin was flooded with fresh or slightly brackish waters from the Paratethys or Sarmatic Sea, a water body covering a large area of central and eastern Europe and represented today by the Black, Caspian, and Aral seas (Fig. 2B, C) (Hsü, 1978; Bianco, 1990).

The present day endemics living in peri-Mediterraean areas have been regarded as Paratethyan-Messinian relicts, separated from the Danubian forms for at least 5 million years (Bianco, 1990). This opinion is shared with Por and Dimentman (1985) for the origin of modern biota in the Mediterranean region.

Recent (Pleistocene and Holocene)

During the Pleistocene, marine regressions occurred at every glacial maximum. River confluences in epicontinental seas and river basins were extended, sometimes far from the present outlets, and linked river basins which at present are independent. In the Mediterranean region, epicontinental seas including the Adriatic and Aegean, were involved. The present day distribution of endemic fishes in ichthyogeographic districts of western Europe (from Tuscano-Latium to Aegeo-Macedo-Anatolian) seems the result of river confluences followed by river isolations that occurred during the last (Würmian) marine regression (about 15-18,000 years ago) (Bianco, 1990). During a fresh or oligosaline phase of the Aegean sea (Fig. 2C), Danubian forms were able to penetrate into several northern Aegean rivers as far as the River Gullück and Koyceviz Lake in Turkey, and the River Sperchios in Greece (Bianco, 1990; Economidis and Banarescu, 1991). The Po extended its basin down to the edge of the Fossa Meso-Adriatica, thereby linking a number of rivers (from the Reno up to Vomano) now isolated. In non-Mediterranean Europe and in Siberia, possibly at every glacial-interglacial ice melting phase, a network of connected lakes and rivers formed (Thunell and Williams, 1983). This allowed primary freshwater fishes (e.g., *Leuciscus cephalus* and *Rutilus rutilus*) to disperse between opposite sides of the northern Paleartic region.

Along valleys, river captures permitted exchanges of cold-adapted species between drainages on opposite sides of a watershed. Recent river captures are known from the western and eastern Alps (Rizzini and Dondi, 1979; Carulli, 1987; Biancotti *et al.*, 1992).

ITALY

Ancient 1 (Middle-Miocene, about 10-15 Ma)

The presence in Italy of the endemic lamprey *Lethenteron zanandreai*, belonging to a genus wide spread in the northern Hemisphere (Holcik, 1986; Almaça and Cortes, 1991), is a dilemma. Normally, freshwater, non-parasitic lampreys correspond in a paired spe-

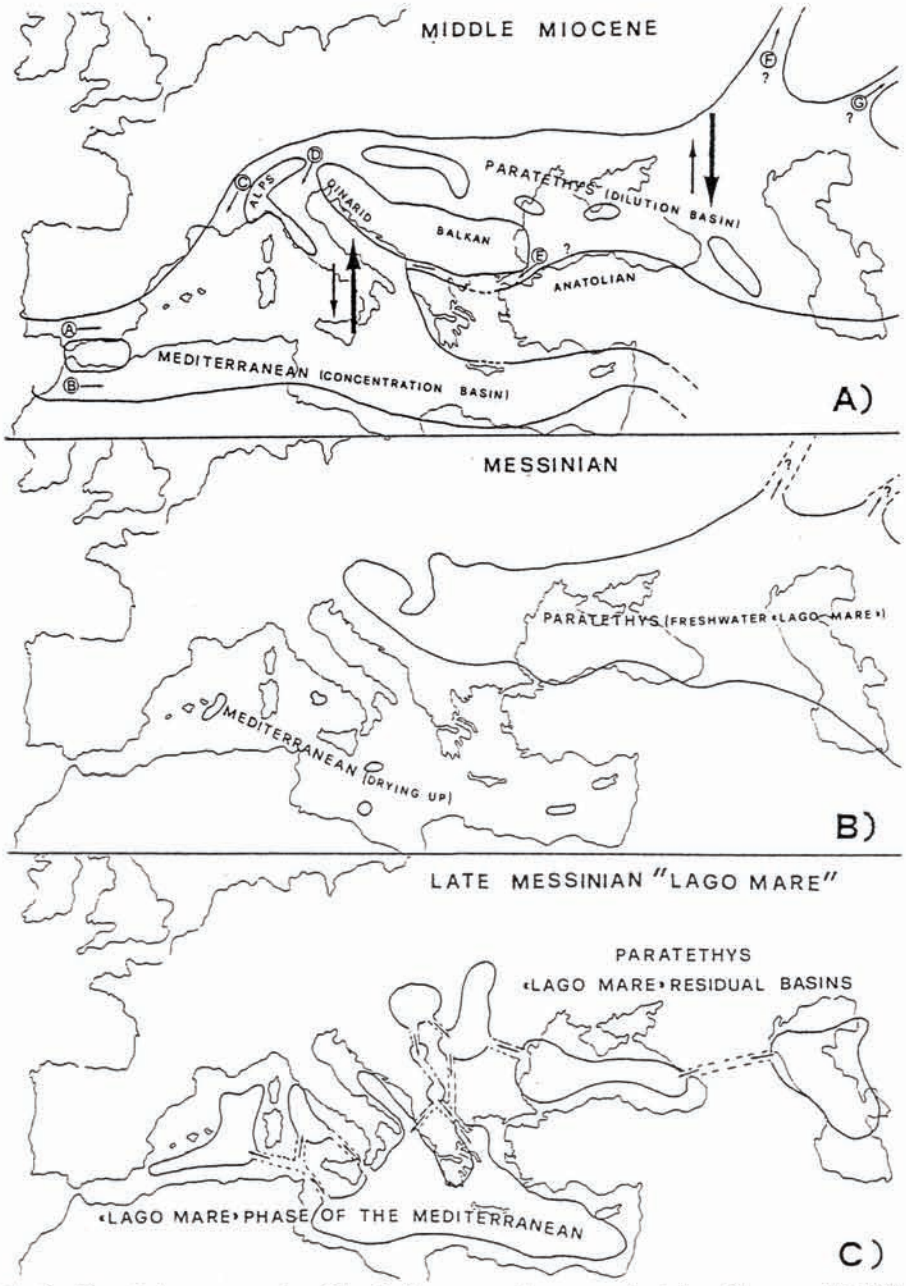

Fig. 2. - Tentatively reconstruction of the Mediterranean palaeogeography during Miocene: A) Middle Miocene (15-20 Ma). The pair of arrows show the Mediterranean negative balance which is documented for Pleistocene (Bethoux, 1979, 1984) and probably exsisted also in Miocene (thick arrow shows prevalence of evaporative losses over atmospheric and river inputs), and dilution in Paratethys. A-G possible sea connections. (D = Adriatic-Pannonian connection). B) The Messinian salinity crisis (about 5.5-5.0 Ma). C) The "Lago Mare" phase of the Mediterranean (about 5.0-4.9 Ma). (From Hsü, 1978 and Bianco, 1990).

cies-complex with migratory, parasitic forms. For the Italian species, the parasitic form is missing. Taxa of the genus *Lethenteron* are cold-adapted and distributed in northernmost Europe. The genus is absent from central and southern Europe where it is replaced by the genus *Lampetra*, but it survives in the Padano-Venetian district of Italy (Bianco, 1992) (Fig. 3).

The Po lamprey, and another endemic fish, the sturgeon *Acipenser naccarii*, probably separated from their ancestors in ancient time. One hypothesis, not supported by paleontological datas, is that they reached the upper palaeoadriatic area via the Adriatic-Pannonian connection (Fig. 2A) during Middle Miocene. It is probable that *Lethenteron zanandreai* represents the relict distribution in southern Europe of a wide-spread genus that was subsequently replaced by *Lampetra* (Fig. 3).

Ancient 2 (Messinian, about 5 Ma)

The oldest fossil record of primary European freshwater fish in Italy, is *Leuciscus oeningensis* Agassiz and dates back to the Messinian (Cavallo and Gaudant, 1987). Other

Fig. 3. - Distribution of genera *Lethenteron* (dotted areas) and *Lampetra* (horizontal bars) in the Euro-Mediterranean sub-region.

records are more recent, for example that of a cyprinid species from the Pliocene of the Arno basin (Azzaroli and Lazzeri, 1977). This suggests that the Messinian was probably the time of first penetration of European-like primary freshwater fish into Italy, but also that the first consistent freshwater fish invasion was recent, in the Quaternary. There are no fossil freshwater deposits rich in primary freshwater fishes in Italy and this suggest a relatively young age for most of the freshwater fishes. In the Mount Amiata (central Italy) fossils of *Barbus* and *Leuciscus* are dated to the Pleistocene (Bradley and Landini, 1982).

Recent

The cold-water species such as *Salmo trutta, Cottus gobio, Phoxinus phoxinus*, and also some moderately cold-adapted species including *Thymallus thymallus* and *Orthrias barbatula*, shared with the Danubian district, probably reached Italy by river captures occurring between river headwaters across the Alps (Rizzini and Dondi, 1979; Carulli, 1987; Biancotti *et al.*, 1992).

The native range of the bullhead, *Cottus gobio*, has been recently identified (Bevagna *et al.*, 1990; Bianco, 1990; Consorzio Regionale Idrobiologia Pesca, 1990). The native range of the bullhead has not been disturbed by human interference. Its probable dispersal history in Italy (Fig. 4) could be applied to other freshwater fishes.

The origin of *Cottus gobio* could be transalpine. It is absent from other Adriatic, Ionian and Aegean districts (Vukovic and Ivanovic, 1971; Economidis, 1991). Consequently, a trans-Balkanic origin is unlikely. The first penetration in Italy probably occurs during the Pleistocene Era. No morphological differentiation has been observed when comparing Danubian, Northern and Central Italian populations (Bianco, pers. obs.). Following its first penetration, the species reached all the cold waters of the Padano-Venetian district during the extended phase of the glacial Po basin. Probably as result of local variation of geomorphology of the crest of the Appennines, causing stream capture between headwaters in central Italy from Pleistocene to the present (Bartolini and Pranzini, 1988; Cattauto *et al.*, 1988), the bullhead reached the headwaters of several of the main rivers (Serchio, Arno and Tiber) of the Tuscano-Latium district (Fig. 4).

Leuciscus souffia muticellus, endemic to Italy (but with related forms in the western Balkans), probably used the trans-Appennine route to reach western Italy (Fig. 5). This moderately cold-adapted riverine fish is an indicator species of the "Thymallus" zone when *T. thymallus* is absent (Dorier, 1957). Other moderately cold-adapted and eurythermal species (*Leuciscus cephalus*, *Barbus plebejus*), common to both districts, probably followed the same route and have similar distributions in Italy.

Warm-water riverine and lacustrine species have more restricted ranges in Italy. There are several endemics restricted to Italy or to Italy and one or more districts of the western Balkan region. Nearly all primary-like freshwater gobies in Eastern Mediterranean districts have restricted ranges. In Italy, *Padogobius martensii* is the biogeographic indicator of the Padano-Venetian district (Bianco and Miller, 1990) (Fig. 6), and *P. nigricans* that of of Tuscano-Latium (Bianco, 1987). These distributions are shared by several cyprinid species including *Chondrostoma genei, Rutilus aula, Chondrostoma soetta,* the loach *Cobitis taenia bilineata* (limited to the Padano-Venetian district), and *Rutilus rubilio* and *Leuciscus lucumonis* which have spread to the Tuscano-Latium district.

Riverine, moderately cold-adapted species, as well as many primary freshwater and warm-waters riverine and lacustrine endemic species, are probably of recent trans-Balkanic

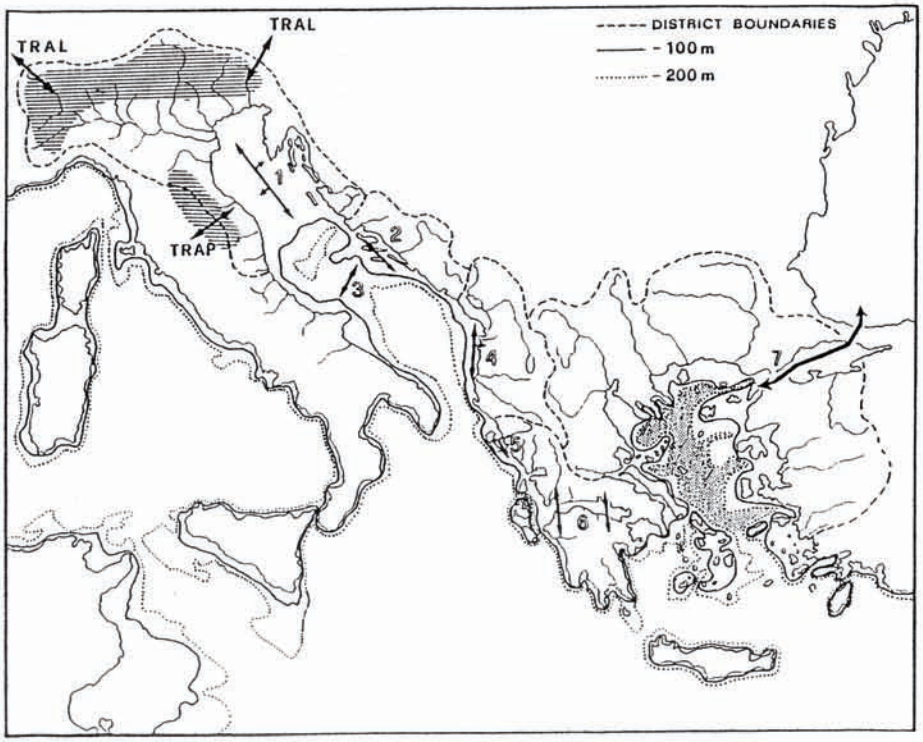

Fig 4. - Present distribution of the bullhead *Cottus gobio* in Italy and western Balkans (horizontal bars) and its probable origin and dispersion during the last glacial marine regressions. TRAL = transalpine penetration; TRAP = transappenninian penetration; 1) the glacial-maxima Po extended basin; 2-7) probable routes of dispersion of primary freshwater fishes by river connections in Italy and western Balkans. Dotted area is the probable freshwater condition reached by the Aegean during glacial-interglacial ice melting phases (modified from Bianco, 1990).

rather than trans-Danubian (transalpine) origins. Several (or their close relatives), are present in Italy and in the western Balkans (Bianco, 1990; Economidis, 1991; Vukovic and Ivanovic, 1971).

In the lowlands, at every glacial maximum, an extended basin of the Po allowed fish-exchange as far as the basin of the River Vomano in central Italy (Fig. 1: 7 and Fig. 4: 1). All fish categories (cold-adapted, moderately cold-adapted and warm-water species) were involved in dispersal events during these periods.

In the Tuscano-Latium district, the rivers Serchio, Arno, Ombrone and Tiber were repeatedly connected and isolated from the Lower Miocene to historic times (Bartolini and Pranzini, 1981, 1988; Cattauto *et al.*, 1988). Today, these rivers are isolated, but their native fish-faunas are identical. The typical endemic species living only in the Serchio, Ombrone, Tiber and Arno river basins is *Leuciscus lucumonis*.

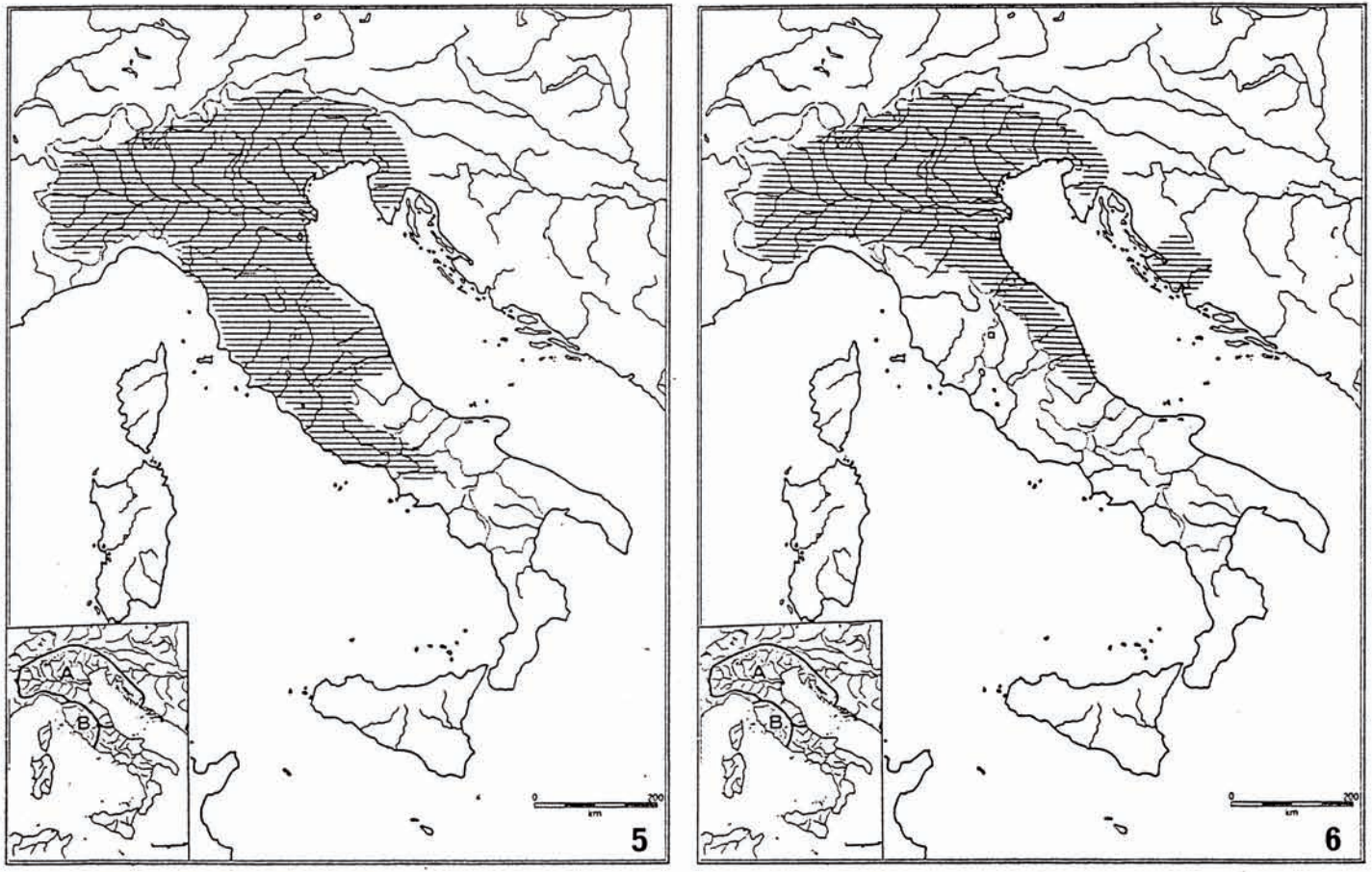

Fig. 5. - The distribution of a moderately cold-adapted riverine species: the Italian endemic *Leuciscus souffia muticellus* (modified from Bianco, 1979). (Inset, the two main districts: A = Padano-Venetian and B = Tuscano-latium).

Fig. 6. - The distribution of a warm-water riverine species: the endemic Padano-Venetian *Padogobius martensii* (from Bianco and Miller, 1990).

FACTORS AFFECTING THE NATURAL DISTRIBUTION OF SECONDARY FISHES

The principal groups of the secondary division of freshwater fishes are the order Cyprinodontiformes and the family Cichlidae. The factors affecting the distribution of the cyprinodontiforms are complex. Most members of this order show high adaptability to extreme environmental, physical and chemical conditions. They are able to survive in hypersaline waters up to a salt concentration of 46-145 ppm (around 1.5-4.5 times that of seawater) (Lee *et al.*, 1980; Hammer, 1986). But this tolerance does not have a counterpart in their distribution patterns. Most species show limited, sometimes patchy, occurrence.

The adaptation to extreme environmental conditions is perhaps a survival strategy adopted by these fishes to escape, or to reduce, interaction with other fishes. Anatolian cyprinodontids (Parenti, 1981) are usually restricted to brackish waters (transitional environments where no true marine or true freshwater fishes are permanent inhabitants), probably thus escaping enemies. Cyprinodontiform fishes may colonize freshwater in the absence of primary freshwater fishes (Darlington, 1957).

The hypothesis that these fishes are sensitive to predators and competitors may be supported by analyzing the reasons for decline or extinction of about 20 species of Cyprinodontiformes, which are mostly the result of the introduction of a predator (*Micropterus salmoides*) or a competitor (*Gambusia affinis*) in their preferred and sometimes isolated habitat (IUCN, 1977; 1988).

Modern Anatolian cyprinodontids (Parenti, 1981) are widespread in peri-Mediterranean countries and in the Near and Middle East, but they did not enter the Black Sea (Steinitz, 1951; Parenti, 1981) (Fig. 7).

Mediterranean

Cyprinodontids are known from the Oligocene of Northern Spain, France and Germany (Gaudant, 1988) and in the Near and Middle East at least since the Miocene (Steinitz, 1951). In northern and eastern Mediterranean countries, they are unknown before the Messinian (about 5 Ma). Most Mediterranean countries were colonized by *Aphanius crassicaudus*, the probable progenitor of the modern *A. fasciatus* (Gaudant, 1979; Sorbini and Tirapelle Rancan, 1979; Chapelle and Gaudant, 1987). The palaeoenvironment consisted of brackish lagoons, where the species was often found associated with other euryhaline species such as gobies and atherinids (Sorbini and Tirapelle Rancan, 1979; Cavallo and Gaudant, 1987). In evaporative basins with hypersaline waters, *A. crassicaudus* was the only fish species present. Fossils of this species have been found to be common in evaporitic Messinian deposits (Sorbini and Tirapelle Rancan, 1979; Gaudant, 1979; Landini and Sorbini, 1989).

The spreading of *Aphanius* was concomitant with the salinity crisis of the Mediterranean, when the basin was reduced to a network of hypersaline lakes with large accumulations of evaporites (Hsü, 1987).

The distribution of evaporitic sites in the Euro-Mediterranean region as well as in the Near and Middle East, from the Middle to Lower Miocene and Messinian (Steininger and Rogl, 1985), resembles that of Anatolian cyprinodontids (Fig. 7). The only evaporitic phase of most of the Mediterranean area was during the Messinian.

In most of the Paratethys area, evaporites do not occur after the Middle Miocene (about 15 Ma). In this ancient sea, the hydrological balance was positive (Bianco, 1990) and never reached hypersaline conditions, at least in the last 10 Ma (Hsü, 1978) (Fig. 2A).

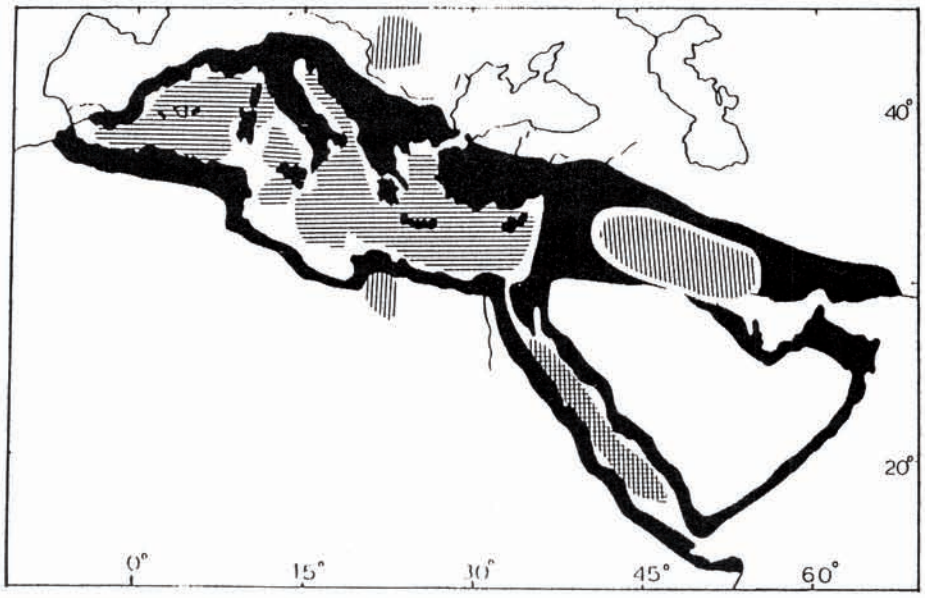

Fig. 7. - Present distribution of "Anatolian cyprinodontids"(*sensu* Parenti, 1981) (black area). Horizontal bars = distribution of Messinian evaporites (about 5.5-5.0 Ma); vertical bars = distribution of pre-Messinian evaporites. Evaporites of both ages are present in the Red Sea (combined from Parenti, 1981; Steininger and Rogl, 1985).

Cyprinodontiformes (at least the Anatolian forms and those with restricted ranges and high salinity tolerance) can disperse in brackish or hypersaline environments in which predators and competitors are scarce or absent. *Aphanius fasciatus*, distributed in central and eastern peri-Mediterranean countries to the Sea of Marmara (including some large islands), has the widest range among Anatolian cyprinodontid species. It was unable to enter the Black Sea (Steinitz, 1951; Parenti, 1981).

Sporadically recorded in coastal seas (Torchio, 1967), *Aphanius fasciatus* is found today in numerous geographically isolated and highly polymorphic populations on costal area of central end western Mediterranean (Boumazia, 1980; Comparini *et al.*, 1983; Tigano and Ferrito, 1985). This suggest that the species has been for a long time in a standing phase of dispersal, and that the environment of the present Mediterranean, regardless the high salinity tolerance of *Aphanius*, is not suitable to its dispersion in western regions. This reinforces the hypothesis that major dispersal events for *A. fasciatus* are related to extreme environmental conditions as was the Mediterranean during the Messinian salinity crisis. Probably other Mediterranean killyfishes of the genus *Aphanius* and the two known species of Valencidae (Bianco and Miller, 1989), are in a static phase of dispersal since the Messinian.

Italy

Secondary freshwater fishes invaded Italy during the end of the Miocene (Sorbini and Tirapelle Rancan, 1979). They were common in nearly all continental Messinian

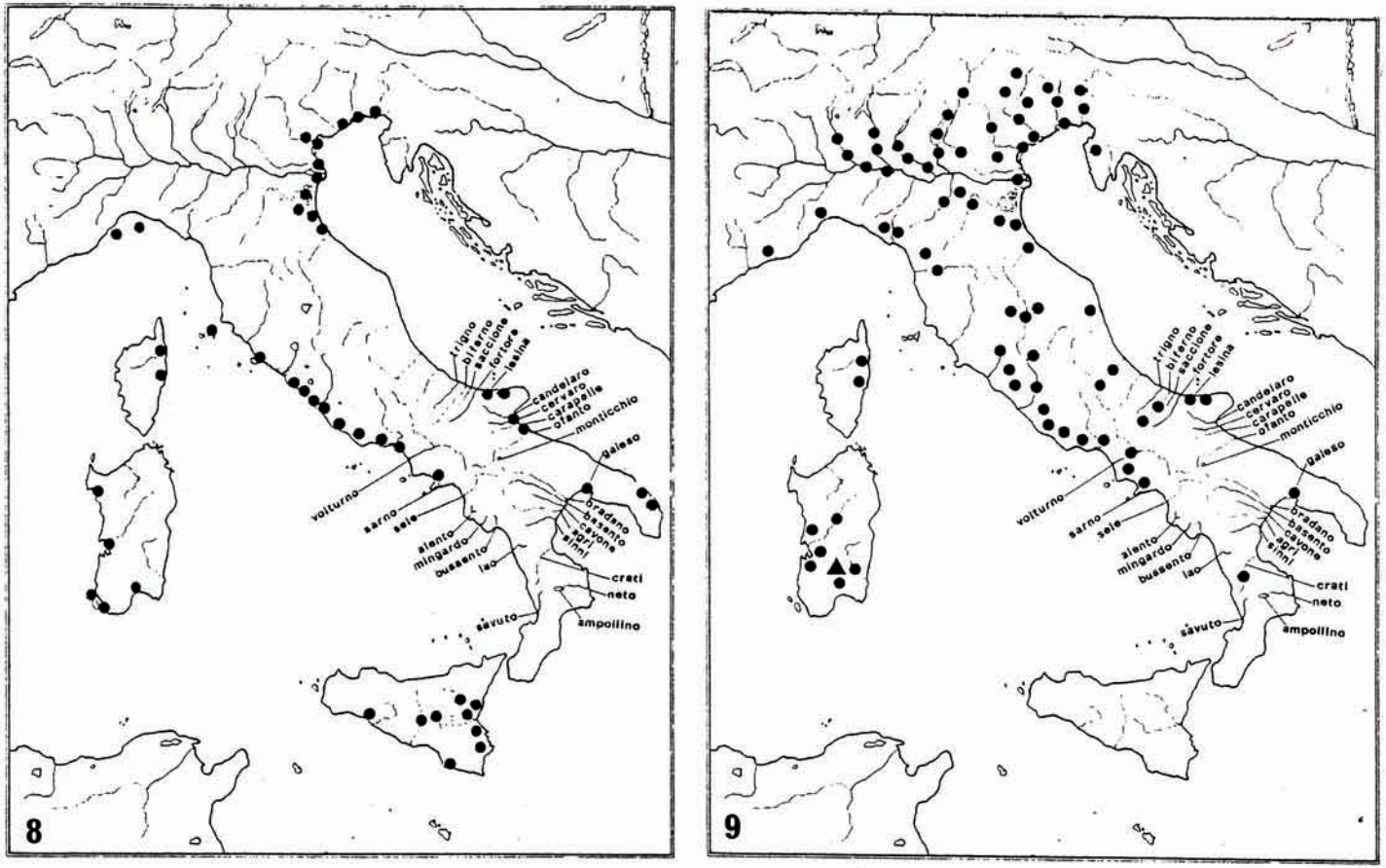

Fig. 8. - Distribution of a "Secondary salt tolerant species" which follows the distribution of transitional environments: *Aphanius fasciatus* in Italy. River names are to show the detailed distribution in southern peninsular Italy (modified from Tigano and Ferrito, 1985).

Fig. 9. - The distribution of a peripheral land-locked species which follows that of available habitats: *Gasterosteus aculeatus*. Spots = *trachurus* phenotype; triangle= *leiurus* phenotype (from Bianco, 1981; Bianco and Taraborelli, 1988).

deposits (Gaudant *et al.*, 1988; Sorbini, 1987; Landini and Sorbini, 1989). The present distribution of *A. fasciatus*, the only native cyprinodontid fish of Italy, follows that of brackish environments (Fig. 8).

Its present status in Italy is unknown, but is probably in progressive decline because of the general destruction of wetlands. The introduction of *Gambusia affinis* had caused its extinction (more than sixty years ago) in several brackish coastal environments of the Latium region in central Italy (Parenzan, 1929).

FACTORS AFFECTING THE NATURAL DISTRIBUTION OF PERIPHERAL FISHES

Peripheral freshwater fishes include the diadromous forms and the recent, landlocked, marine derivates. Nearly all peripheral forms have pan-Mediterranean distributions.

Mediterranean and Italy

In the peri-Mediterranean countries, there are two freshwater species assumed to be of recent marine origin: the three-spined stickleback *Gasterosteus aculeatus*, and the European trout *Salmo trutta*. Their distribution (Fig. 9) tends to follow that of suitable habitats in the mainland and islands. Trout are known in southern Italy since the Pleistocene (Durante, 1978; Bianco and Taraborelli, 1988).

Another peri-Mediterranean freshwater fish, the blenniid *Blennius fluviatilis*, is considered as a Messinian survivor derived from *Lipophrys pavo* (Zander, 1973).

The absence of diadromous populations of trout and stickleback (and also the absence of spawning sites for *Anguilla anguilla*) might have been caused by (a) the probable increase in Mediterranean salinity at each glacial-maximum marine regression and resulting extinction of most marine species including the marine forms of diadromous species (Bianco, 1990), since most benthic and pelagic fishes of the Mediterranean are recent Atlantic derivatives (Quignard, 1978); and (b) the general environmental instability of the Mediterranean basins which has caused massive periodical extinction of biotas (Menzies, 1973), probably due to a combination of factors including increased salinity and recurrence of anoxic events (Thunell *et al.*, 1984).

In Italy, trout have been recorded recently in the sea, near the coasts or in the estuaries, but this seems to be the result of downstream migrations of diadromous stock introduced from northern Europe (Bianco, 1987).

River connections as main routes of dispersion

River connection as an agent in affecting distribution of freshwater fishes may include both river captures and river confluences. River captures between high watersheds (such as in the Italian Alps), may determine exchanges of cold-adapted species between different zoogeographic districts (as between the Danubian and the Padano-Venetian in Italy). River captures across lower watersheds (as in the Appenninian region in Italy) permit the transfer of moderately cold-adapted riverine species. In lowlands, confluence between one or more river basins permit exchanges between previously isolated fish faunas. The freshwater fishes dispersing by river confluences are mostly those living in the middle and lower reaches of rivers, but seasonally cold-adapted species may be involved. Rivers flowing into continental seas are more subject to confluence. During the last Würm glaciation, about 18,000 years ago, there was an estimated panoceanic lowering of sea level by

about 100-130 m below the present (CLIMAP, 1976). River confluences occurring in continental seas with exchanges of fish-faunas, were probably the most important factor in the formation of the modern pattern of freshwater fish distribution in the Old World.

Antropic interference and zoogeographic pollution

Human transfers of species have obscured the native ranges of nearly all freshwater fish of Italy (Bianco, 1995). Introductions are known at least since the Roman Period with the importation into Italy of the Carp, *Cyprinus carpio*, from the Danube basin (Balon, 1969). During the Middle Ages, monks probably introduced other Danubian species (Bianco, 1976), such as *Lota lota, Perca fluviatilis* and *Rutilus pigus* (Bianco, 1987). But the "golden age" for fish transfers started at the end of the past century with the activation of two State Ichthyogenic Centers: that of Rome, in 1895, which had jurisdiction in central, southern and insular Italy and of Brescia, in 1893, which had jurisdiction in northern Italy. During the years 1924-1932, 32 taxa were officially involved in alien transfers by the Rome and Brescia centers, and 16 of them were native taxa including several endemic cyprinids and the crayfish *Austropotamobius pallipes* (Table I) (Ministero Agricoltura e Foreste, 1931). Since the year 1978 the general freshwater fish management passed from the Rome and Brescia centers to each of the 103 Italian provinces which can officially manage their own rivers and fishes. The fish stock used by several provinces includes

Table I. - Number of specimens of native fish taxa (and one species of freshwater crayfish)(x 1,000) transplanted by Rome and Brescia fish-farms between the years 1924-1930. (Data from Ministero Agricoltura e Foreste, 1931).

Species	1924 - 1925	1926 - 1930	
	Roma and Brescia	Roma	Brescia
Anguilla anguilla	15.127	90.006	67.602
Alosa fallax	1.050	11.800	6.100
Salmo carpio	625	112	8.594
Salmo trutta ("stream form")	1.827	6.529	16.973
Salmo trutta ("lake form")	2.586	3.823	23.700
Salmo trutta ("macrostigma form")	-	51	-
Thymallus thymallus	-	20	192
Alburnus alburnus arborella		-	75
Barbus plebejus	89	401	13.446
Chondrostoma genei	-	-	2.300
Rutilus pigus	-	-	630
Rutilus aula	-	-	4.370
Leuciscus cephalus	290	-	5.834
Leuciscus souffia	-	-	3.650
Scardinius erytrophthalmus	-	-	400
Tinca tinca	112	203	1.261
Austropotamobius pallipes	26	101	62

"white fish", a mixture of not well-identified cyprinid species and others. White fish are mostly produced by fish farmers in northern Italy, who use species native to the Padano-Venetian district. The official introduction of "white fishes" caused a process of "padanization" in the basins of the Tuscano-Latium district. An example of official fish management for Siena Province is shown in table II, where white fish were regularly stocked in the Ombrone, Arno and other small rivers of the Tuscano-Latium district, for over 30 years. The fish used were mostly from the same fish farmer (Menozzi from Verona) who used material coming from the Po and Adige rivers and Lake Garda. Interactions between newcomers and local native species in rivers of the Tuscano-Latium district, caused the local extinction or reduction of native fish faunas especially in the main course of rivers and their principal tributaries. Native species are still dominant in small tributaries (Bianco, 1990). The distribution of several species is now radically changed. One of the few undisturbed species is *Leuciscus lucumonis*, which has preserved its original range (rivers Serchio, Arno, Ombrone and Tiber in the Tuscano-Latium district).

Table II. - Nominal species stocked in the freshwaters of Siena Province. The fishes are provided by "Menozzi fish-farm", which rears species coming from lake Garda and Po and Adige rivers. Trout (*Salmo trutta*) are provided from a pisciculture of Trento Province in north Italy. The data have been kindly provided by the Fish Office of Siena province.

Nominal species stocked	Quantity stocked	Locality	Years
Barbus plebejus	"White fish"	Freshwaters of	
Leuciscus cephalus	A mixture of several cyprinid species,	whole province	
Rutilus aula	mostly *L. cephalus* and *B. plebejus*,	(Ombrone and	
Scardinius erythrophthalmus	and a small quantity of other species	Arno river basins)	
Chondrostoma genei	(sometimes unknown)		
Chondrostoma soetta	for the following stock / year:		
Tinca tinca	1.8 - 2.8 tons		1960 - 1983
Other species ?	4.0 tons		1984 - 1993
Salmo trutta	200.000 - 600.000 specimens / year	Trout region	1960 - 1993
Cyprinus carpio	Unknown, transplanted from rice-fields to	public waters	Years "1980"
Anguilla anguilla	Small quantity	Cyprinid waters	1985 & 1986
Esox lucius	Small quantity	Chiusi lake	1986 & 1987
Lepomis gibbosus	Accidentally introduced in whole basins of	Siena Province	
Micropterus salmoides	Unknown	Chiusi lake	1988

Doubtful native species

There are at least three species - *Lota lota, Rutilus pigus* and *Perca fluviatilis* - which are considered to be of doubtful native status in Italy (Bianco, 1987). These mostly lacustrine species, shared with the Danubian district but absent from the western Balkans, are unable to cross mountains by river capture. There are no fossil or archeological records of these species, and their ranges are still expanding. *Rutilus pigus* has been recorded recently, for the first time, in the Po near Turin (Delmastro and Lodi, 1978). This combination of evidence does not support the idea of a natural dispersal of these species into Italy.

They were probably introduced during the Roman period or by monks during the Middle Ages (Bianco, 1987). The pike, *Esox lucius*, is another species widespread in Italy, but its native status, at least in northern Italy, is confirmed by fossils (Sorbini and Durante, 1974).

CONCLUSIONS

The present distribution of native fishes in Italy and other Euro-Mediterranean countries is the result of ancient, recent and contemporary events.

The modern freshwater fishfauna in Italy seems to be not older than Messinian (about 5.0-5.5 Ma) with perhaps the exception of the endemic primary-like lamprey *Lethenteron zanandreai* and the sturgeon *Acipenser naccarii* which probably spread to Italy in the Middle Miocene via the Pannonian-Adriatic connection.

Most of the present Danubian primary or primary-like freshwater fishes in Italy belong to the category of "cold-adapted species" which are very likely of recent trans-Alpine origins.

Nearly all endemic primary and primary-like fishes are warm-adapted lacustrine and riverine species which in Italy probably originated during the "Lago Mare" phase of the Mediterranean. Modern patterns of distributions, often limited to one district or part of it, seems the result of recent, Pleistocene events.

The origin of *Aphanius fasciatus* (secondary freshwater fish) in Italy is Messinian, but since that time the species is probably in a static phase of dispersal.

Peripheral fishes show wider distributions and follow the occurrence of suitable habitats.

Human interference has altered the native ranges of about 70% of the Italian species of freshwater fish.

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